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Identification of the limiting resource within a semi-arid plant association

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Abstract

Our objective was to determine the resource most limiting to plant growth within a semi-arid plant association. We hypothesized that the addition of nitrogen (N) would elicit an increase in biomass more than additions of water, light, phosphorus (P), potassium (K), or sulfur (S). Treatments included the addition of water, N, P, K, or S, or reduction of ambient light on two sites in southwestern Montana within the *Festuca idahoensis*/*Agropyron spicatum* plant association. Nitrogen was the only treatment that increased plant community biomass, specifically native grass biomass (about 50% greater than the control). The addition of water decreased above-ground plant community biomass. Our results suggest that N is the primary limiting resource for the dominant functional group within the *F. idahoensis*/*A. spicatum* plant association.

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1. Introduction

Structure, pattern, and dynamics of plant distributions are affected by abiotic factors such as soil and climate as well as biotic factors including interspecific

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interactions with competitors, mutualists, herbivores, and pathogens (Crawley, 1997, pp. xv–xvii). Understanding mechanisms and processes underlying plant community dynamics provides insight into specific interactions among species or groups of species. These interactions may affect species presence/absence in a community, spatial pattern of species (clumped versus random), water and nutrient status of soils and plants, and niche differentiation (Fowler, 1986).

Interspecific competition for essential resources, such as water, nutrients, and light, is a key force structuring plant communities (Schoener, 1983; Tilman, 1990, pp. 117–141; Wilson and Tilman, 1991) and is the basis for mechanistic models explaining plant community dynamics. For example, the niche differentiation model suggests that through evolution co-existing species have separated along environmental gradients in order to avoid competition for limited resources (MacArthur, 1972). Tilman's R^* theory states that plant community dynamics are driven by species competing for limited nutrients and those species capable of persisting under the lowest soil nutrient concentrations will competitively displace all other species (Tilman, 1982). The mechanisms of competition and fluctuating resource availability were developed into a theory to explain invasion; plant community composition is most susceptible to change when an influx of resources occurs and the intensity of interspecific competition is lessened (Davis et al., 2000).

The *Festuca idahoensis* (Elmer)/*Agropyron spicatum* (Pursh) plant association is widespread throughout the Pacific Northwest and typical of rangeland in western Montana (Mueggler and Stewart, 1980). In other plant associations typical of western grasslands, research has indicated that water is the major limiting resource, with nitrogen (N) and phosphorus (P) having lesser influence (Lauenroth et al., 1978; LeJeune and Seastedt, 2001; Svejcar and Sheley, 2001). The propensity of studies within the *F. idahoensis*/*A. spicatum* plant association that concern species non-indigenous to North America suggests it is at high risk of invasion (Olson et al., 1997; Jacobs and Sheley, 1999; Jacobs et al., 2000; Kedzie-Webb et al., 2002). Therefore, it is important to identify the major limiting resource within the *F. idahoensis*/*A. spicatum* plant association. The occurrence of a specific resource limitation can be incorporated into models of competition between indigenous and non-indigenous species. Such models may be useful for understanding the underlying patterns of invasion, as well as for restoring lands invaded by non-indigenous species.

Our objective was to determine the resource most limiting to plant growth within a *F. idahoensis*/*P. spicata* plant association. We hypothesized that the addition of N would increase plant biomass more than additions of water, P, potassium (K), or sulfur (S). We also hypothesized that a 50% decrease in the amount of ambient sunlight would have no effect on plant growth. Based on prior research and research from others who have worked in more mesic grasslands (Tilman and Wedin, 1991a, b), we believed the *F. idahoensis*/*A. spicata* plant association occurs where water is adequate for survival of semi-arid, native species and N alone limits plant growth.

2. Methods

2.1. Study sites

The study was conducted on two sites in western Montana. Site 1 was located at Redbluff Research Ranch about 2 km east of Norris, Montana (45°35'N, 111°39'W) (hereafter referred to as Redbluff). Elevation is 1505 m, with 305 mm of annual precipitation. Soils are a fine-loamy, mixed, frigid Calcic Argiustoll. Frequently encountered species at Redbluff included *F. idahoensis*, *A. spicatum*, *Stipa comata* (Trin. and Rupr.), *Aristida longiseta* (Steud.), *Chrysopsis villosa* (Pursh) Nutt., *Liatrus punctata* (Hook), *Tragopogon dubius* (Scop.), and *Vicia americana* (Muhl.). Site 2 was located in the Story Hills about 5 km northeast of Bozeman, Montana (45°36'N, 111°34'W) (hereafter referred to as Story Hills). Elevation at Story Hills is 1478 m, with 432 mm annual precipitation. Soils are a clayey-skeletal, mixed Typic Argiboroll. Common plant species at Story Hills included *F. idahoensis* (Elmer), *A. spicatum* (Pursh), *Agropyron smithii* (Rydb.), *Koeleria cristata* (Pers.), *Achillea millefolium* (L.), *Agoseris glauca* (Pursh), *Alyssum alyssoides* (L.), *Artemisia ludoviciana* (Nutt.), *Lomatium ambiguum* (Nutt.), *Lupinus* spp., *Phlox hoodii* (Richardson), *Phlox longifolia* (Nutt.), and *Tragopogon dubius* (Scop.). Both sites were considered late-seral plant communities (Mueggler and Stewart, 1980) (Table 1).

2.2. Experimental design

In spring (Redbluff) and fall (Story Hills) 2000, we applied six essential plant resources to 2.5 × 5.0 m plots. Treatments included the addition or reduction of essential plant resources: (1) water added at a rate of the 50 year average for May, June, and July (plus ambient precipitation) (Table 2), (2) light reduction of 50%, (3) 112 kg N ha⁻¹, (4) 60 kg P ha⁻¹, (5) 112 kg K ha⁻¹, and (6) 112 kg S ha⁻¹. We also included an untreated control. In addition to these main treatments, we addressed potential interactions of water with other essential resources by applying water in combination with all resources except for the untreated control (i.e. double water addition, light reduction plus water, N plus water, P plus water, K plus water, and S plus water).

Water was applied every other week during May, June, and July using backpack sprayers. Light reduction was accomplished during May, June, and July using shade tents with mesh that excluded 50% ambient sunlight. Nutrients were broadcast as granular forms of ammonium nitrate (NH₄NO₃), potassium chloride (KCl), magnesium sulfate (MgSO₄ · 7H₂O), and triple superphosphate (Ca(H₂PO₄) · H₂O)) in a single spring (Redbluff) or fall (Story Hills) application. The complete factorial was arranged in a randomized block design and replicated four times at each site.

2.3. Sampling

Above-ground biomass by species was sampled during peak standing crop 2000 (Redbluff) and 2001 (Story Hills). Above-ground biomass was determined by

Table 1
Surface depth of water (cm) added per month at each site

Site	May	June	July	Total
Red Bluff	6.1	6.6	1.7	14.4
Story Hills	7.7	7.1	1.7	16.5

Table 2
ANOVA *p*-values for main effects and interactions (where applicable)

Source	Total	Grass	<i>Festuca</i>	Forb	Below-ground
Rep	0.079	0.103	0.588	0.075	0.545
Site (s)	0.000	0.833	0.690	0.000	NA
Water (w)	0.043	0.000	0.023	0.795	0.930
Resource (r)	0.000	0.000	0.000	0.622	0.908
w*r	0.636	0.621	0.340	NA	0.219
s*w*r	0.409	NA	NA	NA	NA

Total = total above-ground biomass, Grass = total above-ground grass biomass, *Festuca* = total *F. idahoensis* biomass, Forb = total above-ground forb biomass, Below-ground = total below-ground biomass, NA = not applicable.

clipping plants in three 20 × 50 cm plot frames placed randomly on the ground within each plot. Clipped samples were oven-dried at 60°C for 48 h. Below-ground biomass was sampled at Story Hills in 2001 after above-ground biomass was harvested. Redbluff soils were too rocky for sampling below-ground biomass. Below-ground biomass was sampled by collecting a composite of three soil cores (164.5 cm³) per plot to a 70 mm depth. Roots were carefully washed to remove soil, oven-dried for 48 h at 60°C, and weighed.

2.4. Weather data

Monthly average maximum and minimum temperatures and precipitation data from 1892–2001 (Redbluff) and 1907–2001 (Story Hills) were compiled from the Western Regional Climate Center (NCDC, 2002). Observations were taken from stations located at Norris, Montana (Redbluff) and Montana State University, Bozeman, Montana (Story Hills).

2.5. Statistical analysis

Data were analysed for main effects and interactions using generalized linear model analysis of variance (SPSS, Inc., 1999). Transformations of above-ground biomass were performed to normalize the data and homogenize variances. Data from both sites were pooled because the two sites did not differ in their response to treatments (data not shown). Mean separations were accomplished using Tukey multiple comparison procedure at $\alpha = 0.05$ significance level (Neter et al., 1996, pp. 725–732). Independent sample *T*-tests at $\alpha = 0.05$ significance level were used to

compare means where two factors were present (i.e. site and water addition) (SPSS, Inc., 1999). p -Values are reported for transformed data (Table 1). For ease of interpretation, means of non-transformed data are presented, with means separated by Tukey's poc hoc tests performed on transformed data (Neter et al., 1996).

3. Results

3.1. Climate (average temperature and precipitation)

Average monthly temperatures for Redbluff and Story Hills were within the long-term average (Figs. 1a and b). Average monthly precipitation for 2000 and 2001 was typically similar to or less than the long-term average. Exceptions to this included June 2000 and October 2001 at Redbluff and October 2000 and June 2001 at Story Hills, when average monthly precipitation exceeded the historical average (Figs. 1c and d).

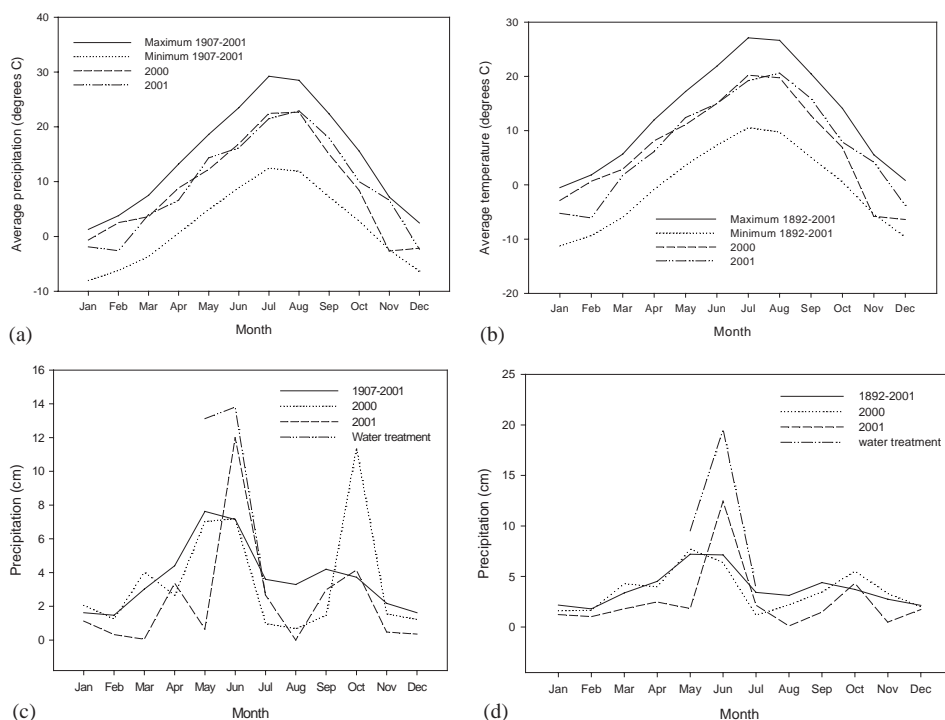


Fig. 1. Monthly temperatures and precipitation at study sites. Long-term monthly average maximum/minimum temperatures and average monthly temperature for 2000 and 2001 at (a) Redbluff and (b) Story Hills. Long-term average monthly precipitation, average monthly precipitation for 2000 and 2001, and precipitation plus water treatment for (c) Redbluff and (d) Story Hills.

3.2. Total above-ground biomass

Total above-ground biomass was affected by the main effects of site, water, and resource treatments (Table 2). Biomass was greater at Story Hills than Redbluff (186.4 vs. 85.7 g m^{-2} ; $p = <0.001$) (Table 2). Water addition decreased total above-ground biomass from 142 g m^{-2} (no water) to 130 g m^{-2} (water addition) ($p = 0.043$) (Table 2). Of all resource treatments, addition of N yielded the highest total above-ground biomass (184.5 g m^{-2}). This was higher than any other resource treatment, but not the control (138.8 g m^{-2}) (Fig. 2).

3.3. Total above-ground grass biomass

The main effects of water and resource treatments affected total above-ground grass biomass (Table 2). Grass biomass was higher in plots that did not receive water (75.4 g m^{-2}) than in plots where water was added (59.5 g m^{-2}) ($p \leq 0.001$). Nitrogen produced the highest above-ground grass biomass, which was about 1.8 times greater than that of the control (Fig. 3). No other treatment was significantly different from the control.

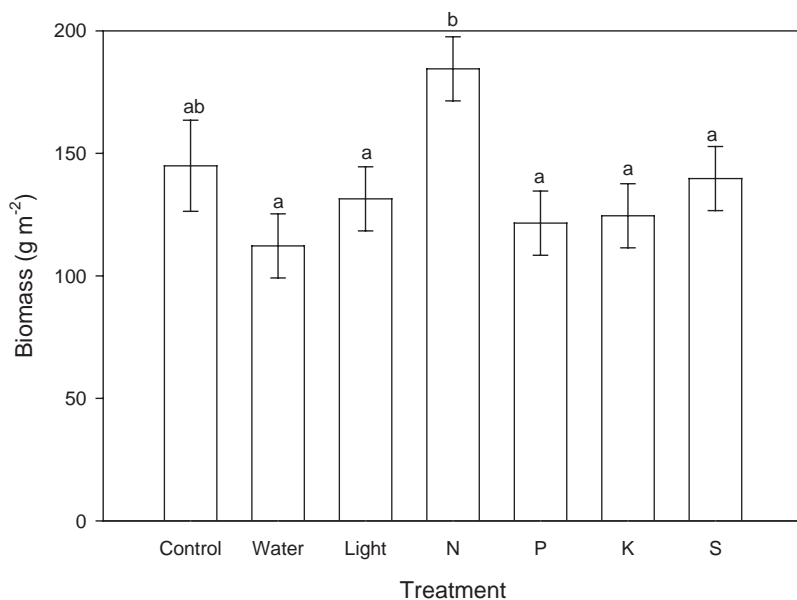


Fig. 2. Total above-ground biomass as affected by resource treatment across sites (data were log₁₀ transformed, but original means are presented). Significant differences are shown with lower case letters. Error bars show mean ± 1.0 S.E.

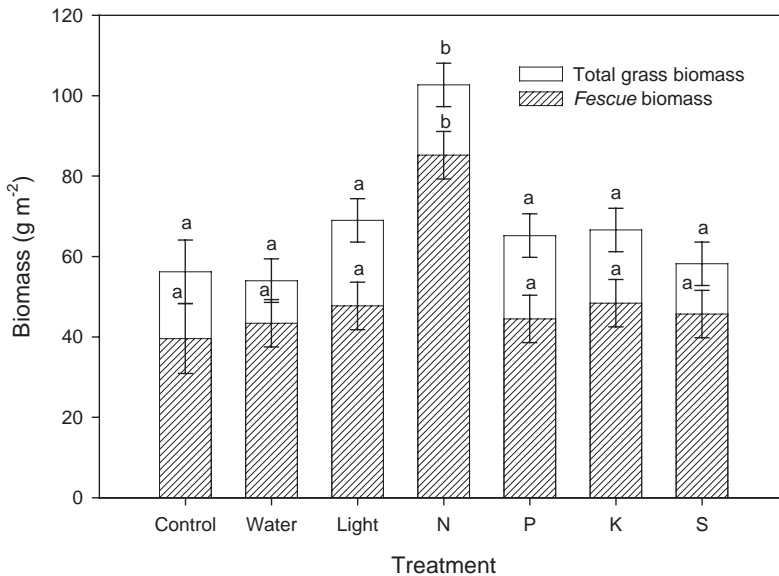


Fig. 3. Total above-ground total grass biomass and *F. idahoensis* biomass as affected by resource treatment (data were square root transformed, but original means are presented). Significant differences within plant groups, across treatments are shown with lower case letters. Error bars show mean \pm 1.0 S.E.

3.4. Total above-ground *F. idahoensis* biomass

We analysed treatment effects on *F. idahoensis* alone because of its widespread occurrence at both sites. The results were similar to total above-ground grass biomass results (Table 2). The main effect of water decreased *F. idahoensis* biomass by 20% compared to the control (56.3 vs. 45.0 g m⁻², respectively; $p = 0.023$). Addition of N increased *F. idahoensis* biomass over that of the control and higher than that of any other treatment (Fig. 3). *F. idahoensis* biomass was 2.2 times greater in plots with N addition when compared to the control.

3.5. Total forb biomass

Total forb biomass was only affected by site. Redbluff forb biomass was substantially lower than Story Hills forb biomass (12.4 vs. 81.2 g m⁻²; $p < 0.001$) (Table 2).

3.6. Total below-ground biomass

Below-ground biomass (at Story Hills only) was not affected by any treatment (Table 2). Values ranged from 0.005 to 0.061 g biomass cm⁻³ soil (mean = 0.021 g biomass cm⁻³ soil).

4. Discussion

Our results indicate that N is the most limiting resource for the dominant functional group in the *F. idahoensis*/*A. spicatum* plant association at the two test sites. This result is consistent with our hypothesis that N would increase plant biomass more than additions of P, K, or S. It is also consistent with other researchers who found N to be the primary limiting factor controlling plant growth (Owensby et al., 1972; Bobbink, 1991; McLendon and Redente, 1991; Tilman and Wedin, 1991a, b; Paschke et al., 2000). Nitrogen is often a limiting factor of plant growth because plants demand relatively large amounts for incorporation into amino acids, proteins, and other nitrogenous organic molecules, such as chlorophyll and hormones (Hopkins, 1995, pp. 101–122). Other major nutrients (P, K, S, Ca, Mg, Mn) originate from soil minerals and can accumulate to a greater extent on soil exchange sites; N, on the other hand, originates from the atmosphere and rarely accumulates on soil exchange sites (Fenn et al., 1998). Nitrogen's high mobility in the soil contributes to its scarcity for plant uptake (Vitousek and Howarth, 1991). Nitrogen limitation can be exacerbated by soil microbes that compete with plants for inorganic soil nitrogen, especially ammonium-N (NH_4^+ -N) (Jackson et al., 1989).

Although the N treatment increased total above-ground biomass more than any other resource addition, the increase was not significantly greater than the control. Typically, soils of late successional plant communities, such as the sites used for this research, have low nutrient concentrations (McLendon and Redente, 1991; Dukes and Mooney, 1999; Paschke et al., 2000). Late successional native species with low nutrient supply often show a limited response to increase in soil nutrients as a consequence of adaptations which promote conservative nutrient use, loss, and uptake (Chapin, 1991; Chapin et al., 1993).

Effects of N addition on biomass were most pronounced in native grasses, especially *F. idahoensis*. In contrast, native forbs did not respond to any resource addition. Our results are consistent with studies where N amendments increased grass biomass without affecting the biomass of forbs (Shaver and Chapin, 1980; Maron and Jefferies, 1999). Growth forms may differ in their nutrient requirement for maximum growth. For example, the tissue calcium concentration at which 90% of the maximum yield is achieved is about twice as high for dicots as for monocots (Loneragan, 1968; Loneragan and Snowball, 1969, as cited in Marschner and Romheld, 1983, pp. 5–60). Response to increased nutrients in plants from low nutrient habitats may be more strongly related to nutrient uptake rates, root distribution patterns, or seasonality of nutrient demands in relation to availability (Shaver and Chapin, 1980). The precise physiological mechanisms for such discrepancies are unknown (Lambers et al., 1998).

Although the sites were characterized as *F. idahoensis*/*A. spicatum* plant associations (Mueggler and Stewart, 1980), the majority of biomass in our study was that of *F. idahoensis*. When analysed separately, *F. idahoensis* responded strongly to N additions. When *F. idahoensis* was excluded from the analysis, resource treatment effects on grass biomass were non-significant. A study in the tall-grass prairies of Kansas showed that net photosynthesis and stomatal conductance of co-

dominant *Andropogon gerardii* and *Sorghastrum nutans* differed in response to water and N additions (Silletti and Knapp, 2001). Combined, these studies suggest that competition models based on limiting resources may be most accurate and predictive when constructed specifically on the dominant species' response. The more dominant the species is in the plant community in regards to contribution to overall biomass, the higher the likelihood of creating competition models that generate accurate predictions on a community wide basis.

The water treatment did not act independently nor did it interact with N to increase plant community biomass. Water did not increase plant community biomass, even though yearly precipitation for 2000 and 2001 were 77% and 74% of average, respectively (NCDC, 2002). One might predict that during drought water availability would be more important than N availability for structuring community dynamics. However, similar outcomes occurred in Colorado where N was most influential in plant community dynamics even in dry years (74% and 77% of average precipitation) (McLendon and Redente, 1991).

Owensby et al. (1972) reported similar results when they added water and N separately and in combination to upland bluestem range in Kansas. Even in a drought year, water and water plus N additions failed to increase above-ground biomass. They theorized that above-ground biomass production may not be directly associated with water availability for a given growing season. Erratic above-ground biomass production as a response to variable precipitation may result in variable accumulation of N at different stages of the N cycle. For example, several years of high precipitation may cause an increase in biomass and high sequestration of N in non-available organic forms. In contrast, a series of years with below normal precipitation could result in an accumulation of available N in the soil. Thus, production may be influenced by previous years' precipitation (Owensby et al., 1972), and not increased by water addition in a given growing season.

Surprisingly, the main effect of water addition decreased total above-ground biomass, native grass biomass, and *F. idahoensis* biomass. We admit that a reduction in biomass with water addition is rather difficult to explain. The *F. idahoensis*/*A. spicatum* plant association is ecologically adapted for survival under a given precipitation regime (35–50 cm yr⁻¹) (Mueggler and Stewart, 1980). Both sites were towards the upper end of the precipitation regime characteristic of the *F. idahoensis*/*A. spicatum* plant association (about 45 cm yr⁻¹); therefore, we speculate that adding water may have elevated water availability beyond the ecological amplitude of the species present at the site and detrimentally affected above-ground biomass. Even though 2000 and 2001 yearly precipitation totals were 77% and 74% of average, respectively, the water treatment increased total precipitation for May, June, and July above the long-term average (Figs. 1c and d). Water not used by the plant community for biomass accumulation may have leached available N beyond the rooting zone of plants, thus limiting N supply and decreasing biomass. This explanation is further supported by the trend of increased plant biomass when N was added but not when N and water were applied together.

There is some evidence that P may limit plant growth in grasslands (LeJeune and Seastedt, 2001). Low concentration (100–3000 mg P kg⁻¹) and water solubility

(<0.01 mg P l⁻¹) of P in soil make it a potential nutrient limiting factor for plant growth in many systems (Sharpley, 2000, pp. D18–D38). We did not find P, or any other resource treatment, to increase total plant biomass over that of the control. This suggests that perhaps in low-resource environments competition may not play as large a role in the dynamics of non-grass species within this plant community.

Based on our findings and the results of other research, we have conceptualized a gradient of plant associations typical of western Montana, progressing from warm and dry to cool and moist climatic conditions (Fig. 4). On the warmer, drier portion of the gradient, water, N, and possibly P appear to limit plant growth (Lauenroth et al., 1978; LeJeune and Seastedt, 2001; Svejcar and Sheley, 2001). Along the cool, moist section of the gradient, water is not limited and N appears to be the major limiting resource (Sollins et al., 1980; Franklin and Halpern, 2000, pp. 123–159; Garrison et al., 2000). The *F. idahoensis*/*A. spicatum* plant association occurs within the mesic portion of the gradient, but where plant associations are still dominated by grasses. Above this point, water becomes more plentiful and trees and shrubs become ubiquitous in plant communities. We believe this plant association occurs along the gradient where water availability is ample and N alone is limiting plant growth.

Competition for N influences plant community dynamics in grasslands more mesic than those of western Montana (Tilman and Wedin, 1991b). It is often assumed that water, not N, is the limiting resource in semi-arid systems. Our results suggest that competition for N, especially among grasses, may be a critical factor even in semi-arid grasslands. The information obtained from this research is a crucial initial step for developing competition models that may be useful for understanding plant community dynamics, including invasions by non-indigenous species.

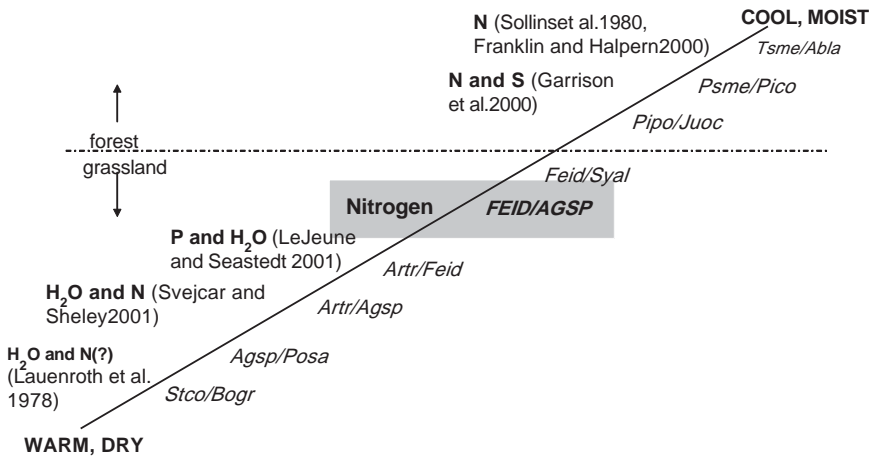


Fig. 4. Limiting resource in various plant associations of western Montana along a moisture and temperature gradient. Plant associations are listed to the right of the diagonal line. Research results identifying limiting resources are listed to the left of the diagonal line.

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